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## Review

# Sex differences in the neural correlates of emotion: Evidence from neuroimaging

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## ABSTRACT

Sex differences in emotional processes represent some of the most robust sex stereotypes worldwide. However, empirical support for these stereotypes is lacking, especially from research utilizing objective measures, such as neuroimaging methodologies. We conducted a selective review of functional neuroimaging studies that have empirically tested for sex differences in the association between brain function and emotional processes (including perception, reactivity, regulation and experience). Evidence was found for marked sex differences in the neural mechanisms underlying emotional processes, and in most cases suggested that males and females use different strategies during emotional processing, which may lead to sex differences in the observed (or subjectively reported) emotional process. We discuss how these findings may offer insight into the mechanisms underlying sex differences in emotional behaviors, and outline a number of methodological considerations for future research. Importantly, results suggest that sex differences should not be ignored in research investigating the neurobiology of emotion.

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## 1. Introduction

Sex differences in emotional behaviors represent some of the most robust sex stereotypes worldwide (Grossman and Wood, 1993; Plant et al., 2000; Timmers et al., 2003). For example, females are often viewed as more emotionally reactive and expressive than males. Indeed, many views of sex differences in emotional behaviors appear to be supported by striking sex differences in the

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prevalence of emotional disorders (Gater et al., 1998). However, empirical evidence on sex differences in specific emotional processes is mixed (Bradley et al., 2001; Fujita et al., 1991; Grossman and Wood, 1993; Seidnitz and Diener, 1998). While there is some evidence for sex differences across a range of emotional processes (i.e., emotion perception, reactivity, regulation and experience), negative findings are also common (Barrett et al., 1998). Further, most research has utilized self-report measures, which are open to language, retrospective and stereotype biases (Fischer, 2000; Fugate et al., 2009).

Neuroimaging research, which provides opportunities for the objective measurement of the neural mechanisms underlying human cognitions and behaviors, has contributed greatly to our knowledge of human emotional processes and the neural systems underlying these processes (e.g., Davidson et al., 2000; Ochsner and Gross, 2008). Thus, using neuroimaging methodologies to investigate sex differences in emotional processes may contribute to current theories of sex differences in emotion that are based largely on more subjective measures. Further, while there has been an interest in understanding the underlying causes of sex differences in emotional processes (Rutter et al., 2003), there is relatively little known about neurobiological mechanisms. Thus, neuroimaging studies of sex differences in emotional processing may also contribute to understanding such mechanisms.

Although few at present, there is a growing number of neuroimaging studies that have investigated the effects of sex on the neural function associated with emotional processes. While there have been some recent reviews that address (1) sex differences in memory and cognitive functions from a neuroscientific perspective (Andreano and Cahill, 2009; Cahill, 2006), and (2) mechanisms underlying sex differences in psychiatry (Rutter et al., 2003), to-date there are no reviews of the neuroimaging literature that focus specifically on mechanisms underlying sex differences in emotional processing in healthy individuals. Thus, the purpose of this review is to provide a synthesis of functional neuroimaging studies that have investigated sex differences in emotional processes. Due to the relatively small number of such studies, and the methodological variation between them, a meta-analysis of results was not considered appropriate. Rather, the aims of this review are to: (1) explore whether the behavioral sex differences reported (or speculated) are supported by functional neuroimaging research; (2) summarize what this research suggests about mechanisms; (3) highlight how neuroimaging findings have prompted some new hypotheses about sex differences in emotional processes; and (4) identify important methodological considerations and limitations, and provide recommendations for future research.

In the following sections, we discuss how neuroimaging research has addressed some key assertions in the literature about sex differences in emotional processes. The general assertions that will be discussed were identified based on those theories that neuroimaging research has specifically set out to test. It is notable, however, that these assertions represent those (1) that are most commonly discussed in the broader literature, and (2) for which there has been some attempts at empirically investigation (Vigil, 2009; Wester et al., 2002). These assertions are as follows. First, females are more emotionally perceptive than males. Second, females are more reactive to emotional stimuli, especially those that are threatening or traumatic. Third, females and males differ in their emotion regulation strategies and efficiency. Fourth, females have a heightened experience of emotions, especially those that are negative.

The empirical studies cited in the following review were selected on the basis that they directly (i.e., statistically) compared brain function between males and females. Because of the interpretive limitations associated with studies that simply report separate results for males and females without directly statistically assessing

these differences, such studies will not be reviewed (Kaiser et al., 2009). Relevant studies were identified via Web of Science and Pub Med search engines. Functional Magnetic Resonance Imaging (fMRI) or positron emission tomography (PET) brain imaging studies were identified (note that we excluded other methodologies such as electroencephalography) that were published or in press before June 2010, where the title, abstract, or keywords included “gender” OR “sex” AND “emotion” OR “affect”, and where research was conducted with healthy control (i.e., no psychiatric) samples. All were conducted with adults unless otherwise stated. Studies were also identified via cross-referencing citations. We placed no restriction on the type of image analysis employed (e.g., whole brain voxel-based versus region of interest). We identified studies investigating aspects of emotional perception (including recognition), reactivity, regulation and experience, and only those investigating what are typically thought of as basic emotions (Bradley and Lang, 1994; Russell, 1980), including happiness, sadness, fear, anxiety, anger, disgust, contempt, and excitement. We excluded studies on hunger, thirst, monetary reward, or pain, as well as social emotions such as empathy, as these constructs are more complex and their discussion was beyond the scope of this paper. The Web of Science search resulted in 1080 papers and the PubMed search resulted in 1315 papers. From these papers, on the basis of the above criteria (plus cross-referencing), thirty two functional imaging studies (employing fMRI or PET) were identified and comprise the basis of the following discussion (see Table 1).

## 2. Females are more emotionally perceptive than males

Females have been found to be more skilled at decoding the emotional dispositions of others (Neff and Karney, 2005; Rosip and Hall, 2004), and more accurate in perceiving emotional prosody and facial expression (Montagne et al., 2005), although there have been some negative findings (e.g., Grimshaw et al., 2004). Such findings have fuelled the suggestion that females are generally more emotionally perceptive than males.

Five neuroimaging studies that have investigated sex differences in the neural correlates of emotional perception were identified. We define emotional perception as the detection of emotional expressions or states in oneself or others. As such, these studies investigated neural activation during the performance of emotion detection or recognition tasks. Two studies reported sex differences in brain activation in the absence of sex differences in behavioral performance. Wildgruber et al. (2002) reported that despite an absence of sex differences in behavioral performance during the discrimination of emotional (sad and happy) vocal intonation, males evidenced significantly higher activation in the right middle frontal gyrus, while females evidenced higher activation in the left middle temporal gyrus. Also, Kempton et al. (2009) reported an effect of sex on brain activation during the recognition of fearful faces, despite no sex differences in task performance; females demonstrated increased activations over males in the left amygdala and right temporal pole, while in males, there were no brain regions demonstrating more activation than in females.

Two studies have reported sex differences in both behavioral performance and brain activation. Han et al. (2008) found that while females responded faster than males during the detection of threat cues in visual scenes depicting dangerous situations, males evidenced stronger posterior parietal activation (and increased connectivity between this region and the medial prefrontal cortex) than females. Hall et al. (2004) found that during recognition of complex cross-modal (visual and auditory) facial expression depicting a range of pleasant and unpleasant emotions, females evidenced greater accuracy in recognition (particularly for sad stimuli) along with more limbic (anterior cingulate and thalamic) activity,

**Table 1**  
Identified studies investigating sex differences in the neural correlates of emotion processes.

Study	N	Stimuli	Emotion of interest	Analysis	Male > Female	Female > Male
<i>Emotion perception studies</i>						
Hall et al. (2004) study 1	16 (8 F)	Faces	Non-specific <sup>a</sup>	WB	R medial frontal gyrus, R superior occipital gyrus	L fusiform gyrus, R amygdala, L inferior gyrus
Hall et al. (2004) study 2	16 (8 F)	Faces & prosody	Non-specific <sup>b</sup>	WB	L inferior frontal gyrus, L inferior parietal gyrus	L thalamus, R fusiform gyrus, L anterior cingulate
Han et al. (2008)	24 (12 F)	Photos	Threat scene (fear)	ROI & WB	L & R posterior parietal cortex	R cerebellum
Kempton et al. (2009) <sup>*</sup>	74 (34 F)	Faces	Fearful face (fear)	WB	R precentral gyrus	L amygdala, R temporal pole, L superior occipital gyrus
Killgore and Yurgelun-Todd (2001)	13 (6 F)	Faces	Fearful face (fear)	ROI	-	-
Wildgruber et al. (2002)	12 (6 F)	Words (audio)	Non-specific <sup>c</sup>	WB	R middle frontal gyrus	L posterior middle temporal gyrus.
<i>Emotion reactivity studies</i>						
Aleman and Swart (2008)	16 (8 F)	Faces	Contempt	WB	L inferior frontal gyrus, L & R medial frontal gyrus, L superior temporal gyrus	-
			Disgust		-	L inferior frontal gyrus, L medial frontal gyrus, L middle frontal gyrus, R precentral gyrus, R superior frontal gyrus, R superior temporal gyrus, L & R parahippocampal gyrus, L & R insula
Azim et al. (2005)	20 (10 F)	Picture cartoons	Happiness	WB	-	R nucleus accumbens, L middle frontal gyrus, L putamen, L & R inferior frontal gyrus, L dorsolateral prefrontal cortex, R caudate
Domes et al. (2010)	33 (17 F)	IAPS pictures	Negative	ROI & WB	-	L & R amygdala, R middle frontal gyrus, R dorsolateral prefrontal cortex, L middle temporal gyrus
Ethofer et al. (2007)	24 (12 F)	Erotic prosody	Excitement	ROI & WB	R superior temporal gyrus (for female prosody)	R superior temporal gyrus (for male prosody)
Fine et al. (2009)	20 (10 F)	Faces (static) & social vignettes (video)	Positive (static)	ROI & WB	R medial frontal gyrus, R superior frontal gyrus, R superior temporal gyrus, R anterior cingulate	-
			Negative (static)		-	-
			Positive (video)		R inferior temporal gyrus, L posterior cingulate	-
			Negative (video)		L middle temporal gyrus	-
Gizewski et al. (2009)	24 (12 F)	Negative (video)	Excitement	L middle temporal gyrus	-	-
Hamann et al. (2004)	28 (14 F)	Erotic pictures	Excitement	ROI & WB	L & R amygdala, R hypothalamus	-
McClure et al. (2004)	17 adults (8 F), 17 adolescents (8 F)	Faces	Angry face (fear)	ROI	-	R orbitofrontal cortex, R amygdala (adults only)
McRae et al. (2008a)	25 (13 F)	IAPS pictures	Negative	ROI	-	-
Sabatinelli et al. (2004)	28 (14 F)	IAPS pictures	Excitement	WB	L & R occipital cortex	-
			Angry face (fear)		-	-
			Threat scene (fear)		-	-
			Disgust		-	-
Schienen et al. (2005)	92 (41 F)	IAPS pictures	Threat scene (fear)	ROI & WB	L & R amygdala, L fusiform gyrus	-
			Disgust		-	-
Shirao et al. (2005)	26 (13 F)	Word sets (visual)	Negative	WB	-	L & R caudate, L putamen

Table 1 (Continued)

Study	N	Stimuli	Emotion of interest	Analysis	Male > Female	Female > Male
Thomas et al. (2001)	12 (6 F)	Faces	Fearful face (fear)	WB	L amygdala attenuation over time	L amygdala persistence over time
Williams et al. (2005)	40 (20 F)	Faces	Fearful face (fear)	ROI & WB	R insula, R inferior frontal gyrus, R amygdala attenuation over time	L anterior cingulate, midbrain, L & R hippocampus, R cerebellum, L amygdala (during early phase of paradigm), R amygdala persistence over time
Wrase et al. (2003)	20 (10 F)	IAPS pictures	Positive	WB	L amygdala, L & R inferior frontal gyrus, L & R medial frontal gyrus, L & R fusiform gyrus	–
			Negative		–	–
<i>Emotion experience studies</i>						
Butler et al. (2005)	23 (10 F)	Visual cue (threat of electrodermal stimulation)	Fear	WB	L postcentral gyrus, R superior frontal gyrus	R midbrain, R insula, R subgenual anterior cingulate gyrus
Caseras et al. (2007)	34 (17 F)	IAPS pictures	Disgust	WB	–	L inferior frontal gyrus, L orbital gyrus, L superior frontal gyrus, L superior temporal gyrus, L middle temporal gyrus L insula
Damasio et al. (2000)	32 (16 F)	Autobiographical recall	Non-specific <sup>d</sup>	ROI & WB	–	–
Drobyshevsky et al. (2006)	31 (15 F)	IAPS pictures	High arousal	WB	Frontal cortex, inferior temporal gyrus, middle temporal gyrus, posterior cingulate, amygdala	Occipital cortex
George et al. (1996)	20 (10 F)	Autobiographical recall	Happiness	WB	–	L inferior frontal gyrus, R cerebellum, L precentral gyrus
			Sadness		–	L middle frontal gyrus, L inferior frontal gyrus, R brainstem, R globus pallidus/putamen
Hofer et al. (2007)	38 (19 F)	IAPS pictures	Positive	WB	–	R posterior cingulate, L putamen, L cerebellum
			Negative		–	L & R superior temporal gyrus, L motor cortex, R supplementary motor area, L lingual gyrus, vermis
Koch et al. (2007)*	40 (19 F)	Odors	Disgust	WB	–	L superior temporal gyrus, R inferior frontal gyrus, L insula
McRae et al. (2008b)	44 (22 F)	IAPS pictures	High arousal	ROI	–	dorsal anterior cingulate
Piefke et al. (2005)	20 (10 F)	autobiographical recall	Positive	WB	L parahippocampal gyrus	R dorsolateral prefrontal cortex
			Negative		L parahippocampal gyrus	R dorsolateral prefrontal cortex, R insula
Schneider et al. (2000)	26 (1 F)	Face pictures	Sad	ROI	R amygdala	–
			Happy		–	–

Wang et al. (2006)	20 (10 F)	emotional movies	Sad & happy <sup>e</sup>	ROI	–	R amygdala
<i>Emotion Regulation Studies</i> Domes et al. (2010)	33 (17 F)	IAPS pictures	Negative increase	ROI & WB	L & R amygdala, L postcentral gyrus, R paracentral lobule, L supplementary motor area, L & R inferior frontal gyrus, L insula, L superior parietal gyrus, L middle frontal gyrus, R lingual gyrus, R cerebellum, R middle temporal gyrus, R hippocampus, R middle frontal gyrus, R superior temporal gyrus, L inferior temporal gyrus, L thalamus, L fusiform gyrus, L precentral gyrus, R precuneus, R superior occipital gyrus	–
			Negative decrease		L superior temporal gyrus, R lateral orbitofrontal gyrus, R anterior cingulate gyrus, R dorsolateral prefrontal gyrus	–
Koch et al. (2007) <sup>a</sup>	40 (19 F)	Odors	Disgust	WB	R middle temporal gyrus, L supramarginal gyrus, L superior occipital lobe	R inferior orbitofrontal gyrus, L amygdala
Mak et al. (2009)	24 (12 F)	IAPS pictures	Positive Negative	WB	L lateral orbitofrontal gyrus L lateral orbitofrontal gyrus, L superior frontal gyrus, R anterior cingulate gyrus, L middle temporal gyrus, L temporal pole gyrus	– L medial orbitofrontal gyrus
McRae et al. (2008a)	25 (13 F)	IAPS pictures	Negative	ROI & WB	–	L amygdala, L ventral striatum, R anterior cingulate cortex, L inferior frontal gyrus, L & R middle frontal gyrus, L superior frontal gyrus, R posterior cingulate gyrus

Note: IAPS = International Affective Picture System, L = left, R = right, ROI = region of interest, WB = whole brain.

<sup>a</sup> Study findings also have implications for automatic emotion regulation.

<sup>b</sup> Responses to happiness, surprise, sadness, anger, fear and disgust were collapsed.

<sup>c</sup> Responses to happiness, surprise, sadness and anger were collapsed.

<sup>d</sup> Responses to sadness and happiness were collapsed.

<sup>e</sup> Responses to happiness, sadness and anger were collapsed.

<sup>e</sup> A mood (happy, sad) by sex (males, females) interaction was tested for R amygdala activity. There was a significant effect of sex but not mood or mood by sex.

while males evidenced more lateral inferior frontal and inferior parietal activity.

Killgore and Yurgelun-Todd (2001) did not test for behavioral differences in an emotion perception study, but found significant sex differences in amygdala activation during happy face perception, whereby males evidenced increased right amygdala activity relative to females.

These studies suggest that regardless of whether sex differences in behavioral performance associated with emotion perception are present, the underlying neural correlates may differ between the sexes. Although it is difficult to make conclusions about discrete emotions (as three of these studies averaged brain activity across emotion types), some patterns of findings are evident across studies. It appears that greater levels of limbic (i.e., amygdala, anterior cingulate, thalamus), inferior frontal and temporal cortex activation were reported in females compared to males, and greater levels of prefrontal and parietal cortical activation were reported in males compared to females. These findings suggest that males and females might recruit different strategies during emotion perception. For example, Hall et al. (2004) suggested that females and males may typically process emotional stimuli at primary versus secondary levels, respectively. According to Damasio (1994) and LeDoux (2000), primary emotions (which arise as a result of processing innately significant environmental stimuli) involve functioning of the limbic system, whereas secondary emotions (evoked by environmental and experiential stimuli that have acquired significance through learning) involve the additional participation of the prefrontal and somatosensory cortices, which also function to modulate limbic system activation. Within this framework, greater limbic activation in females might suggest that emotional perception may be more of the primary than the secondary type, and this may facilitate quicker and more accurate perception. In males, emotional perception may be more impacted upon by regulatory and associative processes, and emotion processing style may be more analytical and potentially slower. How these processing styles might lead to differences in perceptual performance in some, but not all, cases is uncertain and will likely depend on the specific emotion and context (Grimshaw et al., 2004).

Thus, the existing neuroimaging research suggests that females may recruit different brain regions to males during emotion perception. In some cases this may lead to superior perceptual performance, but in other cases this may indicate different underlying neural mechanisms resulting in equivalent performance. Further research is needed to establish whether sex differences in brain activation hold for perception of all emotion types.

### 3. Females are more reactive to emotional stimuli

Females have been found to be more reactive to emotional stimuli, particularly those stimuli that are unpleasant, threatening or traumatic. Greater female reactivity has been found in the domains of self-report (e.g., rating stimuli according to hedonic valence, Lang et al., 1993), behavioral response (e.g., laughing and crying, Vigil, 2009), and physiological responding (e.g., event related potentials, Lithari et al., 2010), although there are also some negative findings (Fugate et al., 2009). There is also some evidence that males may be more physiologically reactive to some pleasant stimuli, especially stimuli of a sexual nature (Allen et al., 2007).

We focus our review of this topic on imaging studies employing passive exposure to emotional stimuli (some of these studies also required participants to make on-line or post-scan ratings of perceived magnitude or intensity of perceived emotion). We identified fourteen neuroimaging studies using such methodology to investigate sex differences in emotional reactivity. Again, studies differ in whether sex differences in behavioral measures were assessed.

Regarding negative emotions, Domes et al. (2010) found that despite no sex differences in valence or arousal ratings of negative picture stimuli, females evidenced greater activity than males to negative versus neutral pictures in the amygdala, right middle frontal gyrus, right dorsolateral prefrontal cortex and left middle temporal gyrus. For more specific negative emotional stimuli, most studies reporting sex differences in activation also tend to find that brain regions are more active in females compared to males (but not vice versa). These studies, which have examined brain activation associated with exposure to words depicting negative aspects of interpersonal relationships (Shirao et al., 2005), disgust facial expressions (Aleman and Swart, 2008), angry face stimuli (McClure et al., 2004) and fearful face stimuli (Thomas et al., 2001; Williams et al., 2005), have typically found increased female activation in subcortical (e.g., thalamus, caudate, putamen), limbic (e.g., amygdala, insula, subgenual cortex) and prefrontal (e.g., superior frontal gyrus, orbitofrontal cortex) regions. Three of these studies examined whether there were sex differences in subjective or other objective measures of reactivity to the emotional stimuli: Shirao et al. (2005) found no sex differences in subjective pleasantness ratings of interpersonal words, although activation of the bilateral caudate nuclei was negatively correlated with these ratings only in females. McClure et al. (2004) found no sex differences in reaction time or threat ratings associated with angry face exposure. Williams et al. (2005) found that although there were no sex differences in post-scan recognition or rated intensity of fearful face stimuli, a persistence of amygdala activity over the course of the fear processing paradigm in females (which differed from a male pattern of quick attenuation of amygdala activity) was associated with greater skin conductance during stimulus processing.

Two studies, however, reported greater male relative to female activation associated with negative stimuli reactivity. Schienle et al. (2005) found that when viewing pictures depicting attacks by humans or animals, although females rated stimuli as more fearful, arousing and negative (post scan), males exhibited greater activation in the bilateral amygdala and the left fusiform gyrus than women. Aleman and Swart (2008) reported greater male than female activation to facial expressions of contempt in the medial frontal gyrus, inferior frontal gyrus, and superior temporal gyrus. It is notable that that stimuli used in these two latter studies might be described as representing cues of dominance, and as such these results may imply a neural basis for higher sensitivity to signals of superiority and interpersonal hierarchy in males than in females.

With regard to positive emotional stimuli, there is some support for sex differences in the neural correlates of stimuli reactivity. Four studies have investigated sex differences in neural response to erotic stimuli. Three of these studies reported greater male compared to female activation during visual presentation of stimuli. Hamann et al. (2004) found that males had a greater response than females in the amygdala and hypothalamus while viewing sexually arousing couple images, despite no sex differences in reported arousal. Sabatinelli et al. (2004) reported greater male than female activation in the occipital cortex during exposure to static images of erotic couples, and Gizewski et al. (2009) reported greater male than female activation during exposure to erotic film excerpts in the thalamus, amygdala, and orbitofrontal and insular cortices. In the fourth study, Ethofer et al. (2007) reported that an enhancement of subjective arousal ratings and middle superior temporal gyrus responses to erotic prosody of opposite (as compared to same) sex voices was similar for male and female participants. This finding contrasts with results obtained in the visual domain, and suggests that increased male reactivity to erotic stimuli may be modality specific.

Regarding other types of pleasant emotional stimuli, three neuroimaging studies have reported sex differences in neural responding. Azim et al. (2005) reported that during exposure to



funny cartoons, despite no sex differences in reported ratings of funniness, females showed greater activation in the nucleus accumbens, putamen, inferior frontal gyrus and dorsolateral prefrontal cortex than males. Given the role of these two latter prefrontal regions in language and executive processing, the authors suggested that females may rely more on these types of skills when perceiving humorous stimuli. Additionally, given the role of the nucleus accumbens and putamen in reward responding, combined with the lack of sex differences in funniness ratings, the authors further suggested that females may have lower expectations of reward during humorous stimuli exposure, and thus react more neutrally when their expectations are exceeded.

Two studies have investigated sex differences in neural responding to more general positive emotional visual stimuli. Wrase et al. (2003) reported that, despite no significant sex differences in self-reported ratings of stimulus valence and arousal, or physiological response (skin conductance or startle modulation), males showed greater brain activity than females in the frontal lobe (inferior and medial frontal gyrus), and amygdala during exposure to positive emotional photo stimuli. Interestingly, although Fine et al. (2009) also found males to show greater activation to positive emotional photos than females in frontal regions (anterior cingulate cortex, medial and superior frontal gyri, and superior temporal gyrus), sex differences were far less pronounced for positive emotional video stimuli.

Thus, although there is evidence that females are more neurally reactive than males to negative interpersonal stimuli, as well as stimuli eliciting disgust, anger and fear, it appears that males may also be more reactive to some classes of stimuli, particularly those stimuli depicting cues of dominance (i.e., contempt, attack scenes).

The specific brain regions found to differ by sex in their level or extent of activation has varied considerably from study to study, which may be due to differences in the specific emotions investigated or differences in methodologies employed. It is of note, however, that three studies implicated the amygdala as being activated more in females than males during reactivity to fearful stimuli (McClure et al., 2004; Thomas et al., 2001; Williams et al., 2005). The amygdala has been implicated in reflexive and unconscious responding to salient and biologically relevant environmental signals, and in producing bodily signs of emotional arousal (LeDoux, 2000). Thus, these findings suggest that females may have a more sensitive fear detection system than males, and it has also been speculated that this may be due to evolutionary adaptation (Williams et al., 2005).

Neuroimaging evidence that males are more reactive to positive emotional stimuli is more limited, and appears to be dependent on the type of positive emotional stimuli and the stimulus modality. Males appear to show greater activation than females to positive visual stimuli (except in the case of humorous stimuli). Sex differences in neural reactivity appear to be less pronounced, however, for positive auditory emotional stimuli, and there is some evidence that the complexity of stimuli (e.g., static versus video visual stimuli) may be important in influencing sex differences in neural responding. However, these interpretations are based on a small number of studies, so replication of these findings is required before more conclusive interpretations can be made.

#### 4. Males are more efficient in emotion regulation

Emotion regulation refers to any process that serves to initiate, inhibit or modulate emotional feelings or behavior. There is some evidence that males and females differ in the type and effectiveness of strategies that they employ to regulate (particularly negative) emotions. For example, females have been found to use more emotion-focused and maladaptive regulation strategies such

as resignation and rumination (Donaldson et al., 2000; Hampel, 2007; Nolen-Hoeksema and Jackson, 2001). Males, on the other hand, use more problem-focused and positive-thinking regulation strategies to deal with negative events (Vingerhoets and Vanheck, 1990).

Three neuroimaging studies have investigated sex differences in the neural correlates of explicit emotion regulation (i.e., studies where participants are instructed to consciously maintain or modulate their emotions). The results of these studies are mixed. McRae et al. (2008a,b) found that despite comparable decreases in self-reported negative emotion in males and females during an effortful emotion regulation task (requiring cognitive reappraisal to down-regulate negative emotion), males showed less increases in prefrontal activation, and greater decreases in amygdala activation than females. These authors speculated that males may expend less effort (i.e., they have less need to use prefrontal-based executive functions) when using cognitive regulation. However, using a similar reappraisal task, Domes and colleagues found greater prefrontal activity in males compared to females during the down-regulation of negative emotion, with no sex differences in amygdala activity or self-reported regulation success (Domes et al., 2010). Whether this indicated that males expended more “effort” during regulation is uncertain, and it is worth noting that whether increased activation in a particular brain region reflects more or less “efficient” processing is currently debated (Poldrack, 2010). Thus, any interpretation of these results should be considered speculative. It is unclear what might account for the discrepancies in the findings of these two studies, but one possible explanation may reside in the fact that the regulation instructions given to participants in each study differed in terms of the types and number of reappraisal strategies suggested. Further, males and females may have used different strategies among or outside of those suggested, but because neither study assessed participants’ self-reported use of regulation strategies, it is difficult to comment further.

Indeed, a third study provides evidence that when given no specific regulation instructions, males and females do use different strategies, and differ in their brain activation. During a task where participants were provided with the general instruction to down-regulate their negative emotional response to emotional stimuli, Mak et al. (2009) found that for the regulation of negative emotion, males displayed stronger activation in the left lateral orbitofrontal gyrus, left superior frontal gyrus, right anterior cingulate gyrus and left middle temporal gyrus and temporal pole. In contrast, females only had stronger activation in the left medial orbitofrontal gyrus compared to males. The authors suggest that the brain regions recruited by females to regulate negative emotion were more associated with emotional processing, while those regions recruited by males were more associated with cognitive processing. This was in line with self-report ratings post-scan, whereby females reported using more emotion-focused coping strategies while males used more cognitive (rational and detachment) coping strategies.

In addition to sex differences in effortful or cognitive emotion regulation, neuroimaging research provides some evidence that there may be sex differences in the more automatic and unconscious emotion regulation processes that are engaged during exposure to emotional stimuli (Gross, 2007). Indeed, seven neuroimaging studies provide support for the suggestion that males may engage in more efficient automatic emotion regulatory processes than females. The studies by Williams et al. (2005) and Thomas et al. (2001), described above, suggest that the mechanism underlying increased reactivity in females to fear stimuli might involve sustained limbic activity, whereas males respond similarly to females initially, but recover more quickly with limbic activity attenuation. That is, in males, regulatory mechanisms might be engaged more quickly to dampen affective reactions. Kempton et al. (2009) reported decreased amygdala activity in males during silent

labeling of fear face stimuli, and suggested that this may reflect greater prefrontal inhibition of amygdala activity associated with automatic emotion regulation that is engaged during explicit emotion labeling. Koch et al. (2007) employed a working memory task during exposure to unpleasant odors, whereby task performance was thought to incur automatic emotion regulatory mechanisms in participants. The authors found that the interaction was associated with greater male activation in a fronto-parieto-cingulate network (parietal and parietal-temporal-occipital areas in particular were activated more than females), whereas females exhibited more activation in the orbitofrontal cortex and amygdala. The authors suggested that these findings imply a weaker automatic emotion regulation system in females, with the pattern of activation in females similar to that often observed with unsuccessful emotion regulation. In males, the interaction was associated with regions typically implicated in successful emotion regulation, suggesting that males might engage in more effective cognitive emotional integration and hence emotion regulation. Indeed, other work by these authors suggests that activation of the fronto-parietal-cingulate network is associated with more effective automatic emotion regulation (Habel et al., 2007).

Thus, a handful of neuroimaging studies support sex differences in the neural correlates of both unconscious (i.e., automatic) and conscious (i.e., effortful) emotion regulation processes. Given the increasing recognition that deficits in emotion regulation are a characteristic feature of a number of mental illnesses for which there are marked sex differences in prevalence and presentation (Gross and Munoz, 1995), further work on sex differences in the neural circuitry of different types of emotion regulation will be important.

## 5. Females experience emotions with greater frequency and intensity

There is some evidence, largely from self-report data, that females experience emotions with greater intensity than males (Brebner, 2003; Vrana and Rollock, 2002). Research has also suggested that whereas females report experiencing both positive and negative affect more often than males, sex differences in self-report are greatest for negative emotions such as fear (Canary et al., 1997; Manstead, 1998) and jealousy (Guerrero and Reiter, 1998).

We identified eleven neuroimaging studies that have investigated sex differences in emotional experience either by instructing participants to try to experience the emotion evoked or portrayed by emotional stimuli, or by inducing an emotional state via autobiographical recall. Two studies employed the former method to investigate neural activation with emotionally arousing stimuli (i.e., collapsing across positive and negative valence). Drobyshevsky et al. (2006) found that during exposure to sex-specific arousing stimuli (i.e., stimuli that were chosen to be equally arousing for males and females), females showed stronger activation than males in the occipital cortex, whereas males had more extensive activation in the frontal cortex, the inferior temporal gyrus, the middle temporal gyrus, the posterior cingulate, and the amygdala. McRae et al. (2008a,b) reported greater anterior cingulate activity in females compared to males during exposure to arousing emotional picture stimuli, although potential sex differences in other brain regions and self-reported arousal were not investigated.

Five studies used emotional picture or video stimuli to induce specific emotions. Hofer et al. (2007) investigated sex differences in neural activation associated with exposure to positive and negative emotional picture stimuli and reported greater female than male activation in a range of regions for both stimuli types. For negative stimuli, females showed more activation in the superior temporal

gyrus, insula, posterior and anterior cingulate cortex, occipital cortex, cerebellum, vermis and putamen (females also self-reported greater felt negative emotion for these stimuli). For positive stimuli, females showed more activation in the right posterior cingulate cortex, putamen and cerebellum. Schneider et al. (2000) found that during sad mood induction (using emotional face stimuli), despite no sex differences in self-reported sadness, males showed greater activity in the right amygdala than females. No sex differences were found for happy mood induction. Wang et al. (2006), on the other hand, found greater right amygdala activity in females compared to males during mood induction (using emotional movies), although the effect was across both happy and sad mood and there was no test for sex differences in self-reported mood. During disgust induction, Caseras et al. (2007) found that females rated disgust stimuli as more anxiety provoking and exhibited more activation in the left ventrolateral prefrontal cortex than males. Butler et al. (2005) investigated sex differences in neural activation associated with anxiety by threatening painful electrodermal stimuli. During anticipation, females showed greater activation than males in the subgenual prefrontal cortex, insula, and brainstem. Males showed more activity than females in the superior frontal gyrus and postcentral gyrus. Subjective reports of anxiety were not assessed.

Findings from the above studies are difficult to interpret due to the range of emotions investigated, and in some cases, the grouping of a range of specific emotions (which may show differential sex differences) into the one analysis (e.g., positive and negative valenced). Some of these studies did not assess sex differences in subjective reports of felt emotion, making it difficult to establish whether neural sex difference were associated with differences in felt emotion versus other cognitive processes recruited to perform the task. However, for negative mood induction, it does appear that in studies that either did not assess subjective felt emotion, or reported greater female subjective report of emotion, females evidenced greater limbic and prefrontal activation than males. Interestingly, those studies where felt-emotion was reported as similar between the sexes tended to report greater levels of limbic and frontal activation in males compared to females, suggesting that although males and females may differ in their frequency and intensity of emotional experience, activity in similar neural circuitry may underlie their emotional experience.

Three studies investigated sex differences in emotional experience using autobiographical recall. For two of these studies, females evidenced greater activation than males in limbic and prefrontal regions during recall of emotional (i.e., across happy, sad, anger, and fear) life events (Damasio et al., 2000) and during induced sadness and happiness (George et al., 1996). In the third study (Piefke et al., 2005), males activated the parahippocampal gyrus to a greater degree than females during both sad and happy recall, whereas females showed more activation in the dorsolateral prefrontal cortex during both sad and happy recall, and more insular activation during sad memory recall. Subjective reports of mood were assessed in two of these studies (George et al., 1996; Piefke et al., 2005), and were found not to differ between males and females, suggesting that the differences in neural activation might be associated with sex differences in strategies used during recall. Indeed, based on their findings, Piefke and colleagues speculate that females may rely more strongly than males on serial ordering of personal past events when recollecting emotionally laden autobiographical experiences, whereas males may rely more on spatial cognition when assessing memories of their personal past. Further, during post-scan briefing, George and colleagues found that the types of events recalled by males and females significantly differed, which may have also contributed to the sex differences found in neural activation.



Studies specifically investigating sex differences in the neural basis for emotional learning and memory (Bremner et al., 2001; Cahill et al., 2004; Canli et al., 2002) provide further weight to these interpretations. In particular, Canli and colleagues assessed brain activation in males and females while they rated their experience of emotional arousal in response to emotionally negative pictures, and then assessed recognition memory for these stimuli three weeks after scanning. Males and females were found to activate different neural circuits to encode stimuli effectively into memory. Females showed better recognition memory, and had significantly more brain regions where activation correlated with both ongoing evaluation of emotional experience and with subsequent memory for the most emotionally arousing pictures. The authors suggested that greater overlap in brain regions sensitive to current emotion and contributing to subsequent memory may be a neural mechanism for emotions to enhance memory more powerfully in females than in males.

In summary, while studies employing autobiographical recall to induce mood showed sex differences in neural activation, evidence from emotional learning studies suggest that these activation differences may be associated with different recall strategies used by males and females, rather than emotional experience *per se*. These findings lend support to the suggestion that some reports in the literature of female greater than male emotional experience may stem from sex differences in neural mechanisms for emotional learning and recall (Fugate et al., 2009).

## 6. Summary

This review highlights that sex differences in the neural correlates of emotion processing are often striking. Although findings were not always consistent, some compelling patterns did emerge. These are illustrated in Fig. 1. Regarding emotion perception, although it is difficult to comment about discrete emotions (because studies often grouped emotions in analyses), emotion perception in general appeared to be associated with greater levels of limbic/subcortical and temporal activation in females compared to males, and greater levels of frontal and parietal activation in males compared to females. These sex differences in neural function could underlie superior performance by females in terms of speed and accuracy associated with emotion detection and recognition. Regarding emotion reactivity, although males and females appear to recruit similar neural circuitry (frontal and limbic/subcortical), there appear to be sex differences in activation dependent on the discrete category of emotional stimulus. Females appear to recruit this circuitry to a greater degree than males during reactivity to a range of negative emotional stimuli (particularly fear), whereas males appear to recruit this circuitry to a greater degree than females during reactivity to positive stimuli as well as negative stimuli signalling cues of dominance or interpersonal hierarchy (i.e., contempt faces and threatening scenes). Although there were too few studies investigating explicit emotion regulation to comment meaningfully on findings, there was evidence that automatic regulation (which likely occurs during emotion reactivity) of negative emotions may involve greater increases in parieto-temporal, and greater decreases in limbic/subcortical areas, in males compared to females, and this may indicate more efficient automatic emotion regulation in males. These findings do lend some support to self-report, behavioral and physiological evidence that females are more reactive to most classes of negative emotional stimuli, whereas males are more reactive to positive stimuli. Regarding emotion experience, although findings are mixed, it appears that males and females may activate similar neural circuitry during emotional experience. Reports in the literature suggesting that females experience negative emotions more

frequently and intensely than males may stem from greater use of autobiographical recall (or possibly rumination, Nolen-Hoeksema, 1990) and concomitant recruitment of the frontal cortex in females.

## 7. Theoretical implications

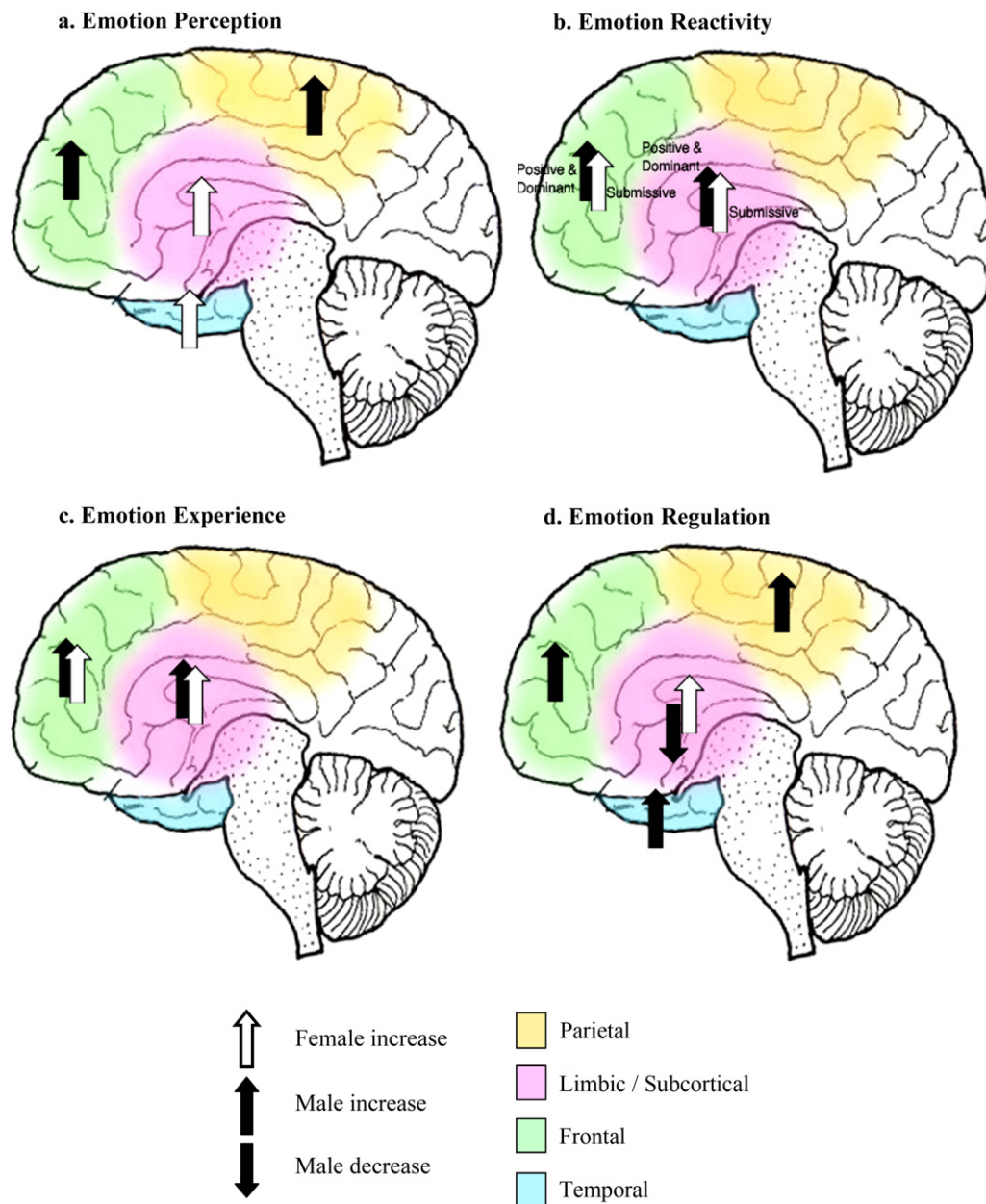
The emotions that females appear to be more neurally “sensitive” to relative to males might be described as submissive or interpersonal in nature (Vigil, 2009), especially with regard to emotional reactivity. On the other hand, males may more readily recruit brain regions to engage in automatic regulation of these negative emotions, but may be more neurally sensitive than females to stimuli signalling cues of dominance or interpersonal hierarchy. These findings are consistent with evolutionary theories that posit that emotional behaviors evolved to promote the attraction and aversion of different types of relationships. For example, social-relational theory (Vigil, 2009) suggests that male and female psychology (and its associated neurobiology) evolved to emphasize the display and/or detection of dominant versus submissive emotional behaviors, respectively. The former are associated with cues of capacity to provide expedient resources or to inflict immediate harm onto others, and are thought to be more important for males who, over evolutionary time, relied more on close interactions with kin, and for whom between-group conflict was frequent. The latter (submissive) emotional behaviors are associated with cues of trustworthiness and are thought to be evolutionarily more important for females, who were more likely to socially migrate and thus needed to be attentive to the possibility of danger and form social bonds with non-kin.

While evolutionary theories provide one explanation as to why males and females may differ in their neural sensitivity to emotional stimuli, experiential or socialization theories are also important to consider. For example, it has been proposed that parents socialize girls to be more relationship-oriented and less instrumental than boys. There is evidence that girls receive more encouragement for dependency and affectionate behavior (Huston, 1983), and that mothers encourage girls (more than boys) to have concern for others, share, and behave prosocially (see Keenan and Shaw, 1997 for a review). Mothers may also be less attentive to girls' assertive behavior (Kerig et al., 1993) and impede the development of girls' sense of mastery by limiting their activities and freedom (Block, 1983).

Although these theories may provide some potential phylogenetic and ontogenetic explanations for the distal origins of the neuroimaging findings, we point out that these theoretical accounts are speculative and that future research is needed to substantiate these ideas. Given that these theoretical positions also relate to emotional experience/expression, future neuroimaging research is especially needed that examines sex differences in these processes as they relate to dominant versus submissive emotions.

## 8. Limitations of existing studies and future directions

This review of sex differences in the neural correlates of emotional processes provides some support for some common assertions in the extant literature regarding sex differences in emotional processes, and also affords insights into some of the potential mechanisms underlying these sex differences while providing support for some existing theoretical accounts. However, there are a number of significant gaps still to be filled. In the following section we offer a summary of the limitations of existing studies, and offer suggestions for future research. We note that our summary of the current gaps is intended to encourage critical review of existing research and thoughtful consideration of research design for future studies. A more in depth discussion of the theoretical and



**Fig. 1.** Summary of sex differences in the neural correlates of emotional processing based on the reviewed studies. For simplicity, locations of brain activation are grouped into four broad regions: frontal, parietal, temporal and limbic/subcortical. Further, we have not distinguished between medial and lateral areas of activation, and the mid-sagittal aspect of the brain is shown for simplicity. (a) Emotion perception: as a number of studies did not assess discrete emotions, there is evidence only for the perception of emotional stimuli in general. (b) Emotion reactivity: although males and females appear to recruit similar neural circuitry, there appear to be sex differences in activation dependent on the discrete category of emotional stimulus (positive versus dominant negative versus submissive negative). (c) Emotion experience: it appears that males and females may activate similar neural circuitry during the experience of emotions. (d) Emotion regulation: there appears to be a neural basis for more efficient regulation of negative emotion in males.

mechanistic considerations associated with each of these issues is also important but is beyond the scope of the current study.

### 8.1. Definitions and measurement of specific emotional processes

Clear interpretation of the findings reviewed is challenging. However, many of the interpretation difficulties are inherent to emotional research (Kober et al., 2008). For example, it is difficult to cleanly separate different aspects of emotional processes. We have suggested that passive exposure to emotional stimuli allows the examination of emotional reactivity, however, it is possible that this type of paradigm incurs other processes such as emotional feeling/experience and automatic regulatory processes. Passive exposure paradigms requiring online ratings of intensity

of perceived emotion might also incur additional processes such as self-awareness and cultural beliefs or norms. Many imaging studies do not employ appropriate controls to disambiguate these different aspects of emotional processing. Thus, better-controlled studies are needed that are clearer about which specific emotional process is being investigated. Below, we suggest strategies that might be employed to aid in this process.

### 8.2. Collection of additional subjective and objective measures

Although it has been suggested that self-reports of emotional reactivity and experience might be subject to biases (e.g., language, memory), these biases are less likely to come into play when reports are obtained in close temporal proximity to the actual emo-

tional response (i.e., they are more likely to come into play when self-report measures draw upon memory of more distant prior emotional experiences, Fugate et al., 2009). Indeed, findings presented above suggest that apparent sex differences in emotional experience, particularly if assessed via recall about past experience, might stem from sex differences in the neural mechanisms of emotional recall. Thus, collection of self-report ratings where applicable (e.g., felt emotion, cognitive strategies used to assist in mood induction or regulation, George et al., 1996), will aid the interpretation of neuroimaging findings. Other more objective measures of emotional processes, such as performance measures (e.g., speed or accuracy) on emotional tasks, or indices of autonomic arousal (e.g., McRae et al., 2008b; Williams et al., 2005) would also be useful for characterizing sex differences in the neural correlates of emotional processes more comprehensively. Studies might also consider the temporal nature (i.e., the time-course) of neural activation associated with emotional processing, which may differ between males and females (Williams et al., 2005).

As noted throughout this review, many imaging studies did not test for self-reported or behavioral sex differences in the emotional process of interest. Without this information, it is impossible to say whether any sex differences in neural activation might cause, or be associated with, a behavioral sex difference. Differences in activation in the context of comparable behavioral performance clearly identify differences in the degree to which one or another brain region was engaged under conditions eliciting comparable performance (Callicott and Weinberger, 2000), and thus may tell us about differences in “strategy” to achieve comparable performance. However, if behavioral differences exist, erroneous activation differences may potentially emerge if behavioral differences are not controlled for. Thus, it has been suggested that in the presence of sex differences in performance or behavior, correlating the performance or behavioral measure with the level or degree of brain activity will allow consideration of sex-related and performance-related changes independently (Casey et al., 2002).

### 8.3. Consideration of laterality

There is evidence that males and females may differ in the lateralization or degree of asymmetry of brain function associated with a range of functions (e.g., Levy, 1977; Nikolaenko, 2005). Indeed, a meta-analysis by Wager and colleagues (Wager et al., 2003) indicated that across the brain, males tended to exhibit a greater degree of lateralized activity than females during affective processing. It is unclear what the implications of this finding are, particularly given that different aspects of affective processing (i.e., recognition, reactivity, experience) and discrete emotions were not separated in the analysis. There is some evidence for sex differences in the lateralization of amygdala function during emotional learning, with males and females employing the right and left amygdala, respectively, to a greater degree (e.g., Cahill et al., 2004), and it has been suggested that this finding might indicate sex differences in global versus local processing strategies (i.e., styles of processing often ascribed to right and left hemisphere structures, respectively). Of the studies reviewed, there were no discernible sex differences in lateralization of brain activity for the different emotions and processes reviewed (see Table 1). Five studies statistically tested for sex differences in lateralization of brain function. All five studies specifically focused on the amygdala. Two of these studies found no sex differences in lateralization of amygdala activity (Schienle et al., 2005; Wang et al., 2006). Two studies found right lateralized amygdala activity in males during sad mood induction (Schneider et al., 2000) and recognition of happy faces (Killgore and Yurgelun-Todd, 2001), somewhat consistent with the emotional memory findings. Williams et al. (2005) found sex by laterality effects of amygdala activity during reactivity to fear faces only when considering

the time-course of neural response. Compared to males, females showed increased left amygdala activity during early response and increased right amygdala activity during late response. Given the current body of literature, sex differences in lateralization of brain activity appear to be important for affective processes and further research on this topic is warranted.

### 8.4. Consideration of sex differences in brain structure, basic function and development

Studies should also consider any sex differences in brain structure, which may impact on interpretation of results (e.g., Pujol et al., 2002). Sex differences in brain structure are well-documented, although not necessarily consistent. One robust finding, however, is that the volume of the total brain is significantly larger in males than females (Giedd et al., 1996), a difference that is observed as early as infancy (Gilmore et al., 2007). Readers should consult other more comprehensive reviews (e.g., Cosgrove et al., 2007) for a summary of other findings. Of particular relevance here is the possibility that the interpretation of functional imaging findings may change once the size of the particular structure implicated is taken into account (Asllani et al., 2009). For example, an activation decrement observed in one group might actually be explained by a corresponding reduction in cortex in that group. A reduction of grey matter might appear as a reduction in measured brain activity due to partial volume averaging effects (Drevets, 1999).

With regard to sex differences in brain activity, sex differences in brain activation associated with very basic functions have been found (e.g., primary visual processing, Levin et al., 1998). Such sex differences may also contribute to any differences noted for emotional processes. Accordingly, studies should consider the unique aspects of processing required by different types of emotional stimuli (e.g., static visual stimuli versus dynamic visual stimuli versus audio stimuli), and consider whether this might have implications for the interpretation of any sex differences in neural correlates found. For example, Fine et al. (2009) investigated sex differences in the neural correlates of emotional perception for both photographic and video stimuli and found that sex differences were less pronounced for video compared to photo stimuli. The authors speculated that male and female neural processing of emotional stimuli may be more similar when conditions more closely approximate real-world environmental conditions.

Brain structure and function undergo rapid and dynamic changes over the childhood and adolescent periods, and sex differences have been found in the development of a number of brain regions (De Bellis et al., 2001; Giedd et al., 1997). Thus, sex differences in brain development may be important to consider in future research, particularly when investigating child and adolescent samples. Killgore et al. (2001), for example, found greater left dorsolateral prefrontal activation with age in female compared to male adolescents during exposure to fear faces, and speculated that this finding might underlie an earlier development of prefrontal cortical emotional regulatory ability in females.

### 8.5. Consideration of sex differences in temperament and personality

Functional imaging studies should consider the potential influence of trait variables (e.g., temperament or personality) on results. Sex differences in such trait variables are well-documented. For example, females appear to exhibit greater affiliative tendencies (Else-Quest et al., 2006), are more sensitive to social-emotional cues (Byrd-Craven and Geary, 2007), and score higher on indices of neuroticism than males (Costa et al., 2001). Males, on the other hand, score higher on facets of sensation-seeking and impulsivity (Else-Quest et al., 2006), and may be less empathic than females



(Byrd-Craven and Geary, 2007). Sex differences in the association between such trait variables and both brain structure and function and have been reported (Hakamata et al., 2006; Whittle et al., 2008; Youn et al., 2002), and could influence sex differences in state measures. Indeed, other research suggests that these variables may have a significant effect on brain function associated with emotional processing (Canli et al., 2001; Caseras et al., 2007; Dickie and Armony, 2008; McRae et al., 2008b; Yücel et al., 2007).

#### 8.6. Consideration of other biological and environmental factors

Considering the influence of other biological (e.g., genetics, hormones) and environmental factors is also likely to be critical to a full understanding of sex differences in emotion. Experimental studies in humans and animals have demonstrated that gonadal hormones have significant effects on resting brain function (e.g., Smith and Zubieta, 2001), and on structural properties of brain tissue such as neuronal size, number, and spacing (Arnold and Gorski, 1984). With regard to emotional functioning, there is evidence that transient sex differences in the effect of hormones on brain function may exist in addition to early appearing and persistent differences. For example, in females, levels of circulating hormones fluctuate cyclically during the estrus cycle, and there is evidence that they have effects on transient brain function (Cosgrove et al., 2007; Derntl et al., 2008; Reiman et al., 1996; van Wingen et al., 2007). Thus, it may be particularly important to consider phase of menstrual cycle in females when investigating sex differences in emotional brain function.

Other research has demonstrated that genes residing upon the sex chromosomes also influence sex differences in neurobiology both directly (i.e., independent of hormones, Craig et al., 2004) and in interaction with gonadal hormones (Davies and Wilkinson, 2006). The emerging field of *imaging genetics* has demonstrated that genotypic variation in certain candidate genes modulates the neural underpinnings of emotional processing, and there is evidence that the effect of such genotypic variation on neurotransmitter activity (Smits et al., 2008; Williams et al., 2003) and behavior (Baca-Garcia et al., 2002; Du et al., 2000) may vary by sex, such that a particular variation in genotype has effects that are stronger for one sex compared to the other.

The environment may also influence sex differences in brain function. There is evidence for this as early as the pre-natal period where, for example, maternal stress may have differential effects on the development of male and female fetal brains (Weinstock, 2007). Researchers are also becoming more aware of the interactive nature of biological variables and the environment in influencing behavior (Boyce and Ellis, 2005; Caspi and Moffitt, 2006; Rutter et al., 2006). Such interactions may be particularly important to consider when interpreting sex differences in the association between neurobiological and emotional processes (e.g., Yap et al., 2008).

### 9. Strengths and limitations of this review

An important strength of this review is that it represents the first attempt to synthesize the existing empirical literature on sex differences in emotional brain function. Secondly, care has been taken to separate out studies addressing different aspects of emotion processing, including perception, reactivity, regulation and experience. Thirdly, only studies where sex differences were statistically tested were included. Studies simply reporting separate tests for males and females are limited in terms of the inferences that can be drawn regarding sex differences, as results obtained from males and females might not necessarily be significantly different from each other. Nonetheless, a few important limitations should be kept in mind. Firstly, only fMRI and PET studies were reviewed. A number of other imaging modalities and methodologies may prove useful in characterizing sex differences in the neurobiology of emotional

processes. Indeed, some research using event-related potentials (Gasbarri et al., 2006) and functional near-infrared spectroscopy (Leon-Carrion et al., 2006) has been conducted that offers insight into sex differences in the temporal course of emotional processing. Other imaging methodologies that allow assessment of structural and functional connectivity may also prove an informative tool for future research. Secondly, the empirical studies included in the review are unlikely to represent a complete set of findings, largely because sex differences (positive or null findings) are often not reported in the abstract or keyword list for a paper, and therefore not easily detected via electronic search. Thirdly, the functional studies reviewed varied widely in their methodologies and statistical analysis techniques. While a meta-analysis of study findings is desirable, the methodological variation between studies is too great to apply such an approach (Eysenck, 1994).

### 10. Conclusions

We have highlighted research showing marked sex differences in the neural correlates of emotional processing. This research offers some support for existing assertions in the broader literature regarding sex differences in emotional processes, and provides clues to the neural mechanisms underlying these differences. Firstly, there is evidence that females might recruit different neurocircuitry to males during perceptual emotion processing, which may in some cases lead to more accurate or faster processing, although in others may result in over reactivity, potentially leading to increased vulnerability to affective disorders (Gater et al., 1998). Secondly, while it appears that females show greater neural activation during reactivity to a range of negative emotional stimuli (particularly involving the amygdala), males show greater activation during reactivity to some classes of negative emotional stimuli that might signal cues of dominance. On the other hand, sex differences in neural activity associated with reactivity to positive emotional stimuli appears to depend on the type of positive emotion and the stimulus modality. Thirdly, a growing number of imaging studies support the suggestion that males and females use different strategies to down-regulate negative emotions, and that these strategies might be mediated by different neural circuitry. Further, some research suggests that males may engage in more efficient automatic or unconscious emotion regulation when exposed to emotional stimuli, which may result from greater integration of cognitive and emotional neural circuits. Fourthly, imaging studies provide some evidence for sex differences in neural activation associated with emotional experience, however it appears in some cases that these differences might stem from sex differences in neural mechanisms for emotional learning and recall, rather than actual emotional experience.

Results from the studies reviewed in this manuscript suggest that sex differences cannot be ignored in neuroimaging research on emotion. Doing so may confound interpretation of results and mask true effects that might be present in only one sex group (Crick and Zahn-Waxler, 2003). Investigating sex differences in the neural correlates of emotion processing might also contribute to a better understanding of sex differences that are observed in a number of psychopathologies marked by deficits in emotional processes. Because of these important implications, more research is needed that (1) aims to replicate the findings discussed in this review, and (2), employs appropriate controls and strategies to aid in the interpretation of significant sex differences if they are found.

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